LAURIDAE: TAXONOMY AND MORPHOLOGY OF ASCOTHORACID CRUSTACEAN PARASITES OF ZOANTHIDS

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ABSTRACT

A provisional list of diagnostic features of the Lauridae and a table of characters distinguishing the contained genera are given. Females of *Laura bicornuta* new species from Hawaii (hosts *Gerardia* sp. and an unidentified zoanthid) and *L. dorsalis* new species from Florida (host *Epizoanthus* sp.) are described and compared with *L. gerardiae* Lacaze-Duthiers from the Mediterranean (host *Gerardia savaglia*). An unnamed female specimen of *Baccalaureus* Broch from Raroia Atoll, French Polynesia (host *Palythoa* sp.) is described; it also serves as the basis for a reinterpretation of tagmosis in that genus, which is thereby shown to require taxonomic revision. The anterior "horns" are interpreted as originally dorsolateral thoracic projections, not homologous with the "filamentary appendages" of *Isidascus* Moyse, for example. Females, males, and a carapace valve of a presumed ascothoracid larva of *Zoanthoecus cerebroides* new genus and species from Hawaii (host *Gerardia* sp.) are described. *Baccalaureus digitatus* Pyefinch is redescribed and assigned to a new, monotypic genus, *Polymarsypus*. Nauplii of *L. bicornuta, L. dorsalis, Z. cerebroides,* and *P. digitatus* are described. Both new *Laura* species and *Z. cerebroides* are occasionally infested with cryptoniscid isopods, *L. dorsalis* by two species. The range extensions of *Laura* and *Baccalaureus* documented here make earlier historical-biogeographical interpretations of this family untenable.

The crustacean subclass Ascothoracida is a wholly parasitic group whose members infest various Echinodermata and Anthozoa. Wagin (1976) monographed the group, and Grygier (1983d) cites most of the taxonomic literature since then. There are now five families, with a revision in progress. The Synagogidae includes several genera parasitizing Antipatharia, Alcyonaria, Ophiuroidea, and Crinoidea. The Dendrogastridae live in the coeloms of Asteroidea and irregular Echinoidea. The single known species of Ctenosculidae lives in a cyst on an asteroid (Grygier, 1983c). The endoparasitic Petrarcidae infest Scleractinia, and the Lauridae, the subjects of this paper, parasitize Zoanthidea.

The two laurid genera recognized to date are *Laura* Lacaze-Duthiers and *Baccalaureus* Broch. Utinomi (1962) placed his genus *Gorgonolaureus* here, but Grygier (1981c) transferred it to the Synagogidae. Okada (1938) thought that *Ulophysema* Brattström should be considered a laurid rather than a dendrogastrid, but no one has followed this suggestion (Grygier, 1982). The only species of *Laura* so far described, *L. gerardiae* Lacaze-Duthiers, parasitizes *Gerardia savaglia* (Bertolini) off Tunisia and Algeria (Lacaze-Duthiers, 1865; 1880; 1883). Knipowitsch (1892) partly redescribed it, particularly the internal anatomy. The 10 described species of *Baccalaureus,* and a few unstudied finds in the literature, live in various zoanthids on reefs and to bathyal depths in the Western Pacific and Indian Oceans (Brattström, 1936; 1956; Broch, 1929; Dawydoff, 1952; Herberts, 1972; Okada, 1938; Pyefinch, 1934; 1936; 1937; 1939; Utinomi and Kikuchi, 1966; Yosii, 1931).

In this paper, two new species of *Laura,* a representative of a new genus, *Zoanthoecus,* and an unnamed *Baccalaureus* specimen are described. Also, Wagin's (1976) suggestion, that the aberrant *B. digitatus* Pyefinch represents a distinct genus, is formally adopted. The distinguishing characters of the four laurid genera recognized here are listed in Table 1.

METHODS

The animals described here were obtained on loan from the National Museum of Natural History, Washington, D.C. (USNM), the British Museum (Natural History) (BMNH), the Muséum National d'Histoire Naturelle, Paris (MNHNP), and the personal collection of Dr. R. Grigg, Hawaii Institute of Marine Biology. Dried specimens were reconditioned overnight in a weak trisodium phosphate solution. Parts of dissected specimens were mounted either in Turtox CMC-10 with acid fuchsin, or unstained in glycerine jelly. Main bodies removed from carapaces were examined whole in lactic acid. Drawings were done with the aid of cameras lucida on a Wild M5 dissecting microscope and a Wild M20 compound microscope. Some type-specimens of various *Baccalaureus* species were briefly examined during visits to the BMNH and the University of Bergen Institute of Marine Biology.

TAXONOMY

Class MAXILLOPODA Dahl, 1956
Subclass ASCOTHORACIDA Lacaze-Duthiers, 1880
Order Lauroidida Wagin, 1976 (pro tem; cf. Grygier, 1983b)
Family Lauridae Gruvel, 1905
Laura Lacaze-Duthiers, 1865
Laura gerardiae Lacaze-Duthiers, 1865
Figure 1a

Material.—Two ♀♀ (MNHNP): coll. H. de Lacaze-Duthiers, 1863, La Calle, Algeria, depth unspecified.

Supplementary Description.—Antennules (Fig. 1a) 3-segmented, second article consisting of 2 fused ones with small anterior seta at midlength. Third article armed distally with long seta posterior to 2 short setae; claw absent and no muscle in that article. Suspected second antennae (Lacaze-Duthiers, 1883) actually exit papillae of maxillary glands. Anterior thoracomeres humped, no lateral or anterior projections. Neither specimen brooding nauplii, so impossible to confirm presence of nauplius eye in larvae (Lacaze-Duthiers, 1883).

Host–Parasite Relations.—Sturaro et al. (1982) reported a high concentration (about 0.3% dry weight) of the arthropod molting hormone ecdysterone in *Gerardia savaglia* and speculated on its origin and biological role. They were unaware of possible *Laura* infestation, stating, ". . . nothing is known about other [besides possible microorganisms] symbionts of *G. savaglia*" and, "Crustaceans are not predators of *G. savaglia.*" It does not seem likely that undetected *L. gerardiae* could be responsible for such a quantity of ecdysterone, even if they were brooding actively molting nauplii, but this possibility cannot be excluded. If the zoanthid produces that hormone itself, the effects on growth and reproduction of *Laura* and the parasite's defenses against hormonal imbalance should be studied.

Laura bicornuta new species
Figures 1b–g, 2

Material.—Holotype ♀ (USNM 204741), 3 paratype ♀♀ (Bernice P. Bishop Museum Cat. No. B507), 14 paratype ♀♀, mostly fragmentary, retained by author: coll. R. Grigg, 12-VIII-1970, Makapuu Pt., Oahu, Hawaiian Islands (21°17.1–19.1'N, 157°32.8'W, 395–425 m); host unidentified zoanthid overgrowing antipatharian *Schizopathes conferta* Brook (ident. R. Grigg). Four paratype ♀♀ (USNM 204742): coll. M. Palmgren, 21-I-1978, Nihoa Bank, Hawaiian Islands (23°16.7'N, 162°37.7'W, 220-241 m); host zoanthid *Gerardia* sp. (ident. R. Grigg) overgrowing unidentified gorgonian.

All had been dried but the holotype, and 2 paratypes from Nihoa Bank.

Diagnosis (♀).—Carapace less than 15 mm in longest dimension, laterally compressed, edges of aperture scalloped. Rosette papillae with 4–8 rounded lobes. Antennules 5-segmented, claw guard with 2 setae. Pair of elongate lobes arising

Table 1. Distinguishing characters of females of the four genera of the Lauridae (plus (+) and minus (−) signs indicate presence or absence of a feature and a combination of symbols (±) means variability among species; a question mark (?) signifies doubt or unavailable information)

Character	*Laura*	*Zoanthoecus*	*Baccalaureus*	*Polymarsypus*
Carapace				
Shape	elongate reniform	ovoid	bilateral sacs, usually coiled	sac-like with many lateral pouches
Texture	stiff	stiff	soft	soft
Aperture protrusion	bulging	bulging	compressed	compressed
Brood chamber	dorsal-ventral	dorsal-ventral	lateral	lateral
Rosette papillae	+	−	−	−
Gut and gonad diverticula	ramifying throughout carapace	ramifying only between carapace pockets	coil with short side branches	?
Body				
Thorax shape	arched	arched	straight	straight
Anterior thoracic horns	±	−	+	−
Antennule form	articulated	articulated	straight	straight
Antennular claw	−	+	?	−?
Frontal filaments/antennae	?	+	?	?
Thoracic chitinous ridge	±	−	+	−
Pleotelsonic spines	−	+	−	−
Furcal rami	short, broad	long, narrow	long, narrow	long, narrow
Thoracopods				
Number of pairs	6	5	4–6	4
Plate-like organ at base of first pair	−	+	+ (some −?)	+
Segmentation of limbs 2–4	2–3	2	1–2	2–3?
Pairs with seminal receptacles	2–5 (sometimes 6)	2–4	2–4	3, 4
Number of seminal receptacles per limb	12–>20	≤5 (additional ones in thorax)	9–11 (Raroia Atoll specimen)	~5

from front of first thoracomere. Large, conical papillae at bases of thoracopods 2–5, some of these limbs 4-segmented, usually not more than 8 spine-like distal setae; more setae on first limb. Vestigial fourth abdominal segment present.

Etymology.—From Latin *bi-* (two) and *cornu* (horn), referring to the protrusions of the first thoracomere.

Description.—Carapace (Fig. 1b, c) dorsoventrally elongated, laterally compressed sac usually about 10–12 mm high, 5 mm long, 3 mm wide (holotype 11.8 mm high, 4.9 mm long, 3.3 mm wide). Anterior side attached lengthwise to axis of host. Vertical opening with interlocking, scalloped lips on protrusion midway along posterior side. Part of carapace dorsal to protrusion larger than ventral part. External cuticle with hollow, columnar, rosette papillae about 30 μm high, 16 μm

Figure 1. a, *Laura gerardiae* Lacaze-Duthiers, antennule; b–g, *Laura bicornuta* new species; b–e, holotype ♀ (USNM 204741); b, carapace attached to antipatharian branch, lateral view, outline of main body dashed; c, carapace, posterior view; d, rosette papillae; e, main body and lip of aperture, lateral view; f, nauplius; g, posterior structures of next naupliar instar within cuticle.

Explanation for all figures: a, antennule; ad, adductor muscle; c, claw guard; d, mandible; f, frontal filament; g, gut diverticulum; gp, genital papilla; h, guard hairs; l, medial languette; n, endopod; o, ovary; oc, oral cone; p, penis; pl, plate-like organ; q, equatorial pores; r, furcal ramus; s, seminal receptacles; v, vestigial somite; x, maxillule; xg, maxillary gland pores. Some thoracopods and thoracomeres numbered for ease of orientation. Scale bars in mm.

across, produced distally into 5–6 (rarely 4, 7, or 8) hollow, rounded lobes (Fig. 1d). Diverticula of gut and ovary ramify throughout carapace.

Main body attached at anteroventral end of posterior protrusion, partly occluding passage between dorsal and ventral chambers, abdomen directed toward opening (Fig. 1b, e). Oral cone and small antennules obscured by powerful adductor muscles. Thorax 6-segmented, segments smaller and narrower posteriorly, each bearing limbs. First thoracomere with pair of ventrally directed, elongate lobes passing anterior to head; lobes rounded distally, covered with sparse, short hairs. First 3–4 thoracomeres humped, more or less thickly setose. Abdomen functionally 4-segmented, but seam visible between telson and vestigial penultimate somite. First abdominal segment wider than last few thoracomeres, bearing penis. Last segment longer and less high than others, with pair of setose furcal rami.

Antennules 5-segmented, about half as long as anterior side of oral cone, which they flank (Fig. 2a). Short first article joined to second by distinct hinge. Second article square, wider than rest; third triangular; fourth twice as long as wide. Distal article subrectangular, with a thick seta, thicker but shorter process (claw guard) with terminal and subterminal seta, another short seta, and several small bumps; claw absent.

Oral cone pear-shaped. Posterior margins of labrum meeting, but readily separable. Mandibles long, narrow, with fine setae along lateral edge, and dense, retrorse hairs along distal part of medial side (Fig. 2b). Maxillules blunt, triangular (Fig. 2c). Maxillae tapered, fused medially for half of length, tips blunt, bifid (Fig. 2d). Short medial languette may be present below mouth, but not seen in dissected preparations.

Thoracopods uniramous. Description based on right limbs of wet-preserved paratype; setation of dried specimens similar, but articulations less clear. First limb (Fig. 2e) biarticulate, first article longer, with 1 outer seta; about 10 short setae on second article. Large genital papilla at base of limb. Second and third limbs triarticulate: coxa, basis, exopod (Fig. 2f–h); basal part of coxa produced into conical papilla where narrow ducts from numerous, pear-shaped seminal receptacles exit; fine hairs over most of limb, several short setae at tip. Fourth and fifth limbs much like preceding 2 pairs, but exopod biarticulate, with fewer distal setae (Fig. 2i–k). Sixth limb lobular with fine hairs and seminal receptacle (Fig. 2l).

Penis uniramous, tapered, with dense setae to each side of base (Fig. 2m). Furcal rami trapezoidal, longer than high, with numerous simple or compound spines along ventral margin, smaller ones distally along dorsal margin, cuticular ctenae along dorsal margin and distally on faces, 4–6 thick terminal setae no longer than rami, sometimes few shorter medial or dorsal setae (Fig. 2n).

Developmental Stages.—Eggs and nauplii found together in carapace of 2 wet-preserved individuals including holotype, nauplii most abundant. Brood present in poor condition in some dried specimens.

Eggs yellow, nearly spherical, about 0.2 mm across.

Nauplii (Fig. 1f) pear-shaped, tapered posteriorly, 0.44 mm long, 0.28 mm across (mean of 19). Eyeless, with frontal filaments, labrum, 3 pairs of limbs, and ventral spines. Armament of next instar clearly visible beneath cuticle. Band of pores encircles body at midheight (equatorial pores).

Frontal filaments simple, cylindrical, arising anteromedial to antennules. Labrum oval, reaching posteriorly beyond mandibles. Mouth opening present.

Antennules uniramous, indistinctly divided into about 5 articles; distal article

Figure 2. *Laura bicornuta* new species; a, f–n, holotype ♀ (USNM 204741); b–e, dried paratype ♀ (author's collection); a, antennule; b, mandible; c, maxillule; d, maxillae; e, first limb and genital papilla; f, tip of second limb; g, h, third limb and detail of tip; i, j, fourth limb and detail of tip; k, tip of fifth limb; l, sixth limb; m, penis, anterior view; n, furcal ramus, lateral view. For explanation see Figure 1.

with 1 short and 2 long setae; penultimate article with 2 medial setae, 1 lateral one; next 2 proximal articles with 1 medial seta each. Antennae biramous with biarticulate protopod. Coxa and basis each with 2 enditic spines, thicker one of each pair containing rudiments of 2 spines in next instar. Exopod 8–9-segmented, distal articles with 5 natatory setae. Endopod 3-segmented; first article with 2 enditic spines; second article with 2 unequal medial setae; terminal article with 3 setae, one shorter than others. Mandibles similar to antennae but smaller, exopod with only about 7 articles and 4 setae, presence of thinner spine on coxal endite uncertain.

Ventral spines large, containing 2 unequal pairs of setae of next instar (Fig. 1g), anterior pair longer than posterior. Posterior end of body conical with fine hairs, enclosing 3 pairs of triangular lobes and long terminal seta of next instar.

Associated Fauna.—The specimens from Nihoa Bank parasitized the same zoanthid colony as *Zoanthoecus cerebroides* new genus and species, described below. Two specimens from Nihoa Bank, and 3 from Makapuu Pt. contained hyperparasitic cryptoniscid isopods of an undescribed species, but of a genus apparently the same as found by Pyefinch (1939) in *Baccalaureus japonicus* (=*B. pyefinchi* (Brattström, 1956)) at Zanzibar (Cattley, unpubl. MS on Isopoda of John Murray Expedition). Not all the dried *Laura* were examined for isopods, so the true infestation rate is probably higher.

Remarks.—The carapace of *L. bicornuta* is similar in shape to *L. gerardiae,* but the latter is larger, with a long axis of 2–4 cm. The rosette papillae on the carapace do not have long, tapered points like *L. gerardiae.* The latter has no indication of the compound nature of the last abdominal segment and no thoracic projections except humps. The antennule is better developed in *L. bicornuta.* In *L. gerardiae* the first limbs are the longest, but not in *L. bicornuta,* where they are more setose as well. The seminal receptacle duct papillae are more rounded in *L. gerardiae,* none of limbs 2–4 are 4-segmented, and there are more terminal setae on them. Seminal receptacles have not been recorded in the sixth limb of any ascothoracid till now, although *L. dorsalis* new species, described below, sometimes has one there. *Laura bicornuta* often has more furcal setae than *L. gerardiae.*

The nauplii are indistinguishable from those of *L. gerardiae* (Lacaze-Duthiers, 1883; Knipowitsch, 1892), even to the armament of the next instar, which corresponds to the nauplius of *Baccalaureus japonicus* Broch (Yosii, 1931). However, Lacaze-Duthiers (1883) described a colored nauplius eye not seen in the present material.

A pair of anterior thoracic protrusions has till now been considered one of the characteristics of *Baccalaureus,* where they are usually long and coiled. Although they are comparatively poorly developed in *L. bicornuta,* other characters such as carapace shape and armament, and appendage morphology, now take on greater importance in distinguishing the genera (Table 1).

Laura dorsalis new species
Figures 3, 4

Material.—Holotype ♀ (USNM 204743), 3 paratype ♀♀ (USNM 204744): coll. off Miami, Florida, 24-VIII-1964, *Gerda* sta. G-354 (25°39'N, 79°32'W, 800–830 m); parasites of *Epizoanthus* sp. (ident. C. Arneson) overgrowing gorgonian *Paramuricea* cf. *echinata* Deichmann (USNM 56041). In an earlier paper (Grygier, 1981b) the gorgonian itself was mistakenly listed as the host.

Diagnosis (♀).—Carapace more than 5 mm in longest dimension, bulbous, edges of aperture entire. Rosette papillae with 2–10 triangular fins. Antennules superficially 4-segmented with spine-like claw guard. Transverse dorsal frills on thoracomeres 1 and 2, lateral lobes of first bent anteroventrally.

Etymology.—From Latin *dorsum* (back), referring to the elaborations of the first 2 thoracomeres.

Description.—Carapace similar to other *Laura* species, but longer and broader relative to height (Fig. 3a). Holotype 10.8 mm high, 6.4 mm broad, dorsal chamber 7.6 mm long, ventral one 4.8 mm long. Dissected paratype 8.2 mm high, 4.4 mm wide, about 5.1 mm long. Aperture on protrusion below midheight along posterior side, with smooth, unscalloped margins.

Figure 3. *Laura dorsalis* new species; a–c, e–g, holotype ♀ (USNM 204743); d, paratype ♀ (USNM 204744); a, carapace, lateral view; b, rosette papillae; c, main body, dorsal view; d, main body and aperture lip, lateral view; e, antennule; f, mouthparts except maxillae; g, maxillae. For explanation see Figure 1.

Carapace attached by anterior side to gorgonian axis, covered with zoanthid polyps; opening in zoanthid cover that exposes aperture hard to locate even when correct orientation established. One empty gall completely enclosed, similar to cysts left by dead *Gorgonolaureus muzikae* Grygier (1981b).

Hollow rosette papillae covering carapace radiate distally into 2–10 (mostly 4–9, 40% with 5) hollow, triangular fins (Fig. 3b). Papillae with 5 fins are 26 μm across, those with 8 or more are 39 μm across.

Main body oriented with dorsum of head and thorax overreaching oral cone and facing ventrally (Fig. 3c, d). Consists of head, 6-segmented thorax, and 4-segmented abdomen with furca. Body of holotype 3.0 mm long excluding protrusions of first thoracomere, 3.0 mm high, 1.4 mm across frill of second segment.

Antennules shorter than oral cone, which they flank, superficially 4-segmented (Fig. 3e). First article short, broad. Second twice as long as wide, slimmer than first, musculature and faint creases showing origin by fusion of 3 articles. Third article (homologous to fifth of other ascothoracids) narrower and shorter than second, slightly tapered. Distal article slightly shorter than third, bearing short, thick spine, short seta, and longer, thicker seta. Position of muscle anterior to thick spine refutes possible homology to claw in other ascothoracids (apparently completely regressed here); this spine actually the claw guard.

Oral cone as long as deep. Rear margins of labrum meeting but readily separable. Tip produced into little spout. Mandibles longer and thinner than maxillules, former with medial, retrorse hairs, latter a naked triangle (Fig. 3f). Maxillae much larger, fused for 60% of length, with tips divided into distal prong and movable posterior hook (Fig. 3g). Medial languette short and wide (Fig. 3f). Openings of maxillary glands on maxillae behind edges of labrum. Pair of large, thin-walled swellings containing maxillary glands on vertical, ventral surface between oral cone and limbs. Adductor muscle at level of these glands above oral cone; gut diverticula and gonads pass into carapace anterior to adductor muscle, and ramify extensively.

First 2 thoracomeres with trilobed dorsal frill scattered with short, stiff setae. Middorsal lobe of first one poorly developed, lateral lobes longer than high and bent forward along dorso-ventral axis of carapace, resembling thoracic lobes of *L. bicornuta,* but shorter. Frill of second segment smaller, with equal middorsal and lateral lobes. Other thoracomeres with progressively smaller humps. Ventral edges of tergites marked by distinct line of thick chitin.

Six pairs of thoracopods, first and second about equally long, others progressively shorter, sixth much shorter than rest. First limb cylindrical, narrow, perhaps 3-segmented (second article longest) with several spine-like distal setae (Fig. 4a); large female genital papilla at its base. In thoracopods 2–5, coxae over half of length (Fig. 4b), containing 10–20 flask-shaped seminal receptacles with long, narrow ducts opening on low swellings at bases of limbs. Tiny seta dorsal to swellings in at least some cases. Basis square or slightly longer than wide. Distal article (remnant of exopod) triangular, little longer than wide, with 10–15 short setae at tip and in subterminolateral cluster (Fig. 4c). Fine hairs and cuticular ctenae present on limbs, less abundant than *L. bicornuta.* Sixth limb 2-segmented, first article broad, sometimes with seminal receptacle, second article cylindrical, 2–3 times as long as thick, with few tiny distal setae (Fig. 4d).

Sperm expressed from seminal receptacles with elongate heads 23 μm long, tails at least 80 μm long (Fig. 4e).

First abdominal segment rectangular, with wrinkled, uniramous penis rudiment on anterior (ventral) side (Fig. 4f). Next 3 segments trapezoidal, dorsal sides short. Evidence of fusion of erstwhile fourth and fifth segments much less obvious than in *L. bicornuta.* Furcal rami trapezoidal, 60% longer than high, tapered distally (Fig. 4g); armed with relatively weak, ventrolateral cuticular ctenae, 4 distal setae half to two-thirds as long as rami, sometimes a few mediodistal setae.

Eggs, Larvae, Associated Fauna.—Holotype with 32–35 eggs, 6 nauplii, and 2 cryptoniscid isopods; paratypes with, respectively, eggs, empty brood chamber, and 1 cryptoniscid isopod and eggs.

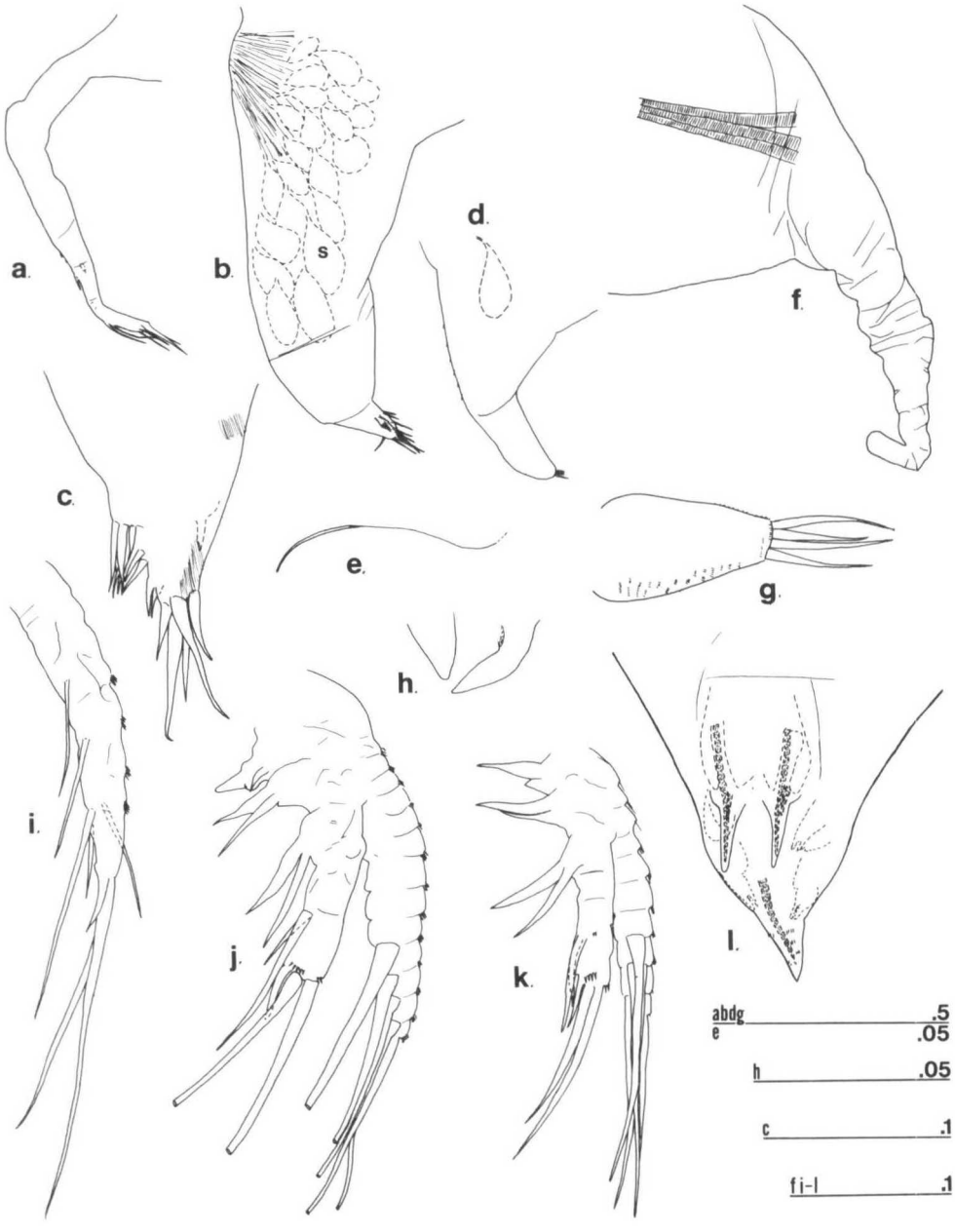

Figure 4. *Laura dorsalis* new species; a–f, holotype ♀ (USNM 204743); g, paratype ♀ (USNM 204744); a, first limb; b, second limb; c, tip of third limb; d, sixth limb; e, spermatozoon; f, penis, lateral view; g, furcal ramus, lateral view; h–l, nauplii; h, frontal filaments; i, antennule; j, antenna; k, mandible; l, posterior end of body, including subcuticular structures of next instar (setae stippled). For explanation see Figure 1.

Eggs spherical, 0.24 mm across.

Nauplii very similar to those of *L. bicornuta.* Pear-shaped, 0.48 mm long, 0.29 mm wide. Frontal filaments present (Fig. 4h), no nauplius eye. Labrum twice as long as wide. Antennules (Fig. 4i), antennae (Fig. 4j), and mandibles (Fig. 4k) as in *L. bicornuta,* but with heavier, spinule-like cuticular ctenae on outer edge of each article. Coxal endites smaller and blunter than basal or endopodal ones, 1 spine much smaller than other. Rear end of body as before, but 3 pairs of subcuticular lobes seem to have invaginations (Fig. 4l).

Cryptoniscid isopods in holotype are new species assignable to same undescribed genus as hyperparasites of *L. bicornuta* and *B. pyefinchi.* Isopod in paratype is of different, undescribed genus.

Remarks.—*Laura dorsalis* is smaller than *L. gerardiae,* but much more bulbous, and the rosette papillae are quite different. The antennules are better developed in *L. dorsalis.* The sperm in *L. gerardiae* are supposed to be 10 μm long (Lacaze-Duthiers, 1883), versus over 20 μm just for the heads in *L. dorsalis.* Lacaze-Duthiers probably did not see the flagella, which are characteristic of ascothoracid sperm (Grygier, 1981a; 1982).

Laura dorsalis differs from *L. bicornuta* in the relatively much broader carapace with slightly different rosette papillae, and in the anterior thoracic modifications. There is no distinct remnant of the fourth abdominal segment. The degree of antennular reduction and the shape of the claw guard are different. The first limb is longer in *L. dorsalis.* Limbs 2–5 have much less prominent seminal receptacle duct papillae, and are all 3-segmented. The limb setae are arranged like *L. gerardiae* rather than *L. bicornuta.* The 2-segmented sixth limb is unique to this species.

Baccalaureus Broch, 1929
Baccalaureus sp.
Figure 5

Material.—♀ (USNM 210851): coll. J. P. E. Morrison, Raroia Atoll, Tuamotu Archipelago (no other data); within polyp of zoanthid *Palythoa* sp. (USNM Acc. No. 210851).

Description.—Maximum length of carapace (mantle) 8.0 mm, height 8.3 mm, width 5.8 mm. Two helical lateral lobes, with slightly greater vertical than horizontal diameter, and medial lobe containing main body (Fig. 5a, b). Medial lobe 4.6 mm long, 3.5 mm high, protrudant posterior end compressed with vertical aperture. Lateral lobes originate above medial lobe, but ⅔ of their bulk below midheight of latter, turning 1¾ revolutions; shallow, radial indentations corresponding to spaces between major branches of gut diverticula. Cuticle studded with small, conical, perforated papillae. Aperture lined with short guard hairs (Fig. 5c); 3 more rows of hairs within opening. Outer row only loosely attached to mantle; thus guard hairs possibly represent adherent parts of exuvia. Mantle coils filled with yellow, subspherical eggs 0.22 mm in greatest diameter (mean of 21).

Main body about 3.9 mm long, excluding anterior horns (Fig. 5c). Head broadly attached to anterior and lateral sides of medial lobe, especially by powerful adductor muscles. Antennules extending posteriorly from origins anterodorsal to oral cone. Oral cone like that of *Laura* in side view, but more compressed laterally. Ventral body surface between oral cone and thoracopods produced into pair of semicircular lobes containing maxillary glands. Six thoracic segments of equal length and uniform width. First with pair of large, anteroventrally directed, distally

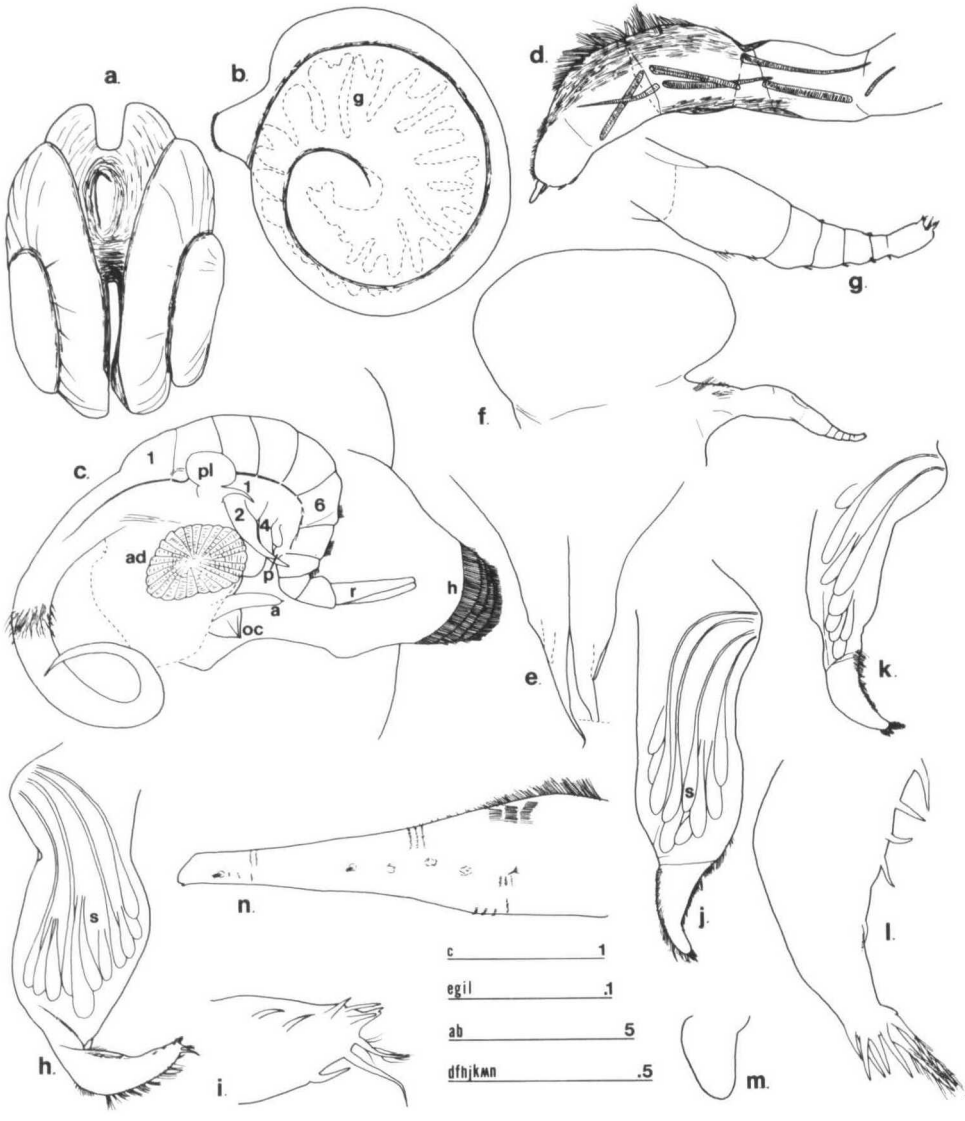

Figure 5. *Baccalaureus* sp. ♀ (USNM 210851); a, b, carapace, posterior and lateral views; c, main body and aperture, lateral view, only partial setation of anterior horns shown; d, antennule; e, maxillae; f, first limb and plate-like organ; g, detail of tip of first limb; h, i, second limb and detail of tip; j, third limb; k, l, fourth limb and detail of tip; m, fifth limb; n, furcal ramus, medial view. For explanation see Figure 1.

tapered horns covered with fine hairs and coiling around columellae of lateral mantle lobes. Sixth thoracomere with patch of short dorsal setae. Cuticle thickened at ventral margins of tergites, forming chitinous ridge from middle of sixth segment anteriorly onto basal part of horns. Five pairs of thoracopods, superficially corresponding to thoracomeres 2–6, but probably really belonging to segments 1–5 (see Remarks).

Abdomen 4-segmented. First segment largest, with posterodorsal patch of short

setae; posteroventral penis rudiment. Third and fourth segments less high; patch of short setae on posterior surface of second segment dorsal to third. Fourth segment with pair of long, tapered furcal rami directed toward mantle opening.

Antennules slightly curved, blunt, and functionally unsegmented, but traces of 6 original articles visible (Fig. 5d). Armed distally with large, blunt spine (homology to claw or claw guard unclear), and 3 small setae; much of surface covered with fine hairs.

Maxillae only prominent paired mouthparts found, fused medially for much of length; bifid tips with long, attenuated distal prongs, much shorter posterior ones (Fig. 5e). Short medial languette present.

First pair of thoracopods arising below chitinous ridge, directed posteriorly with flat, oval, basal plate 0.64 mm long, 0.40 mm high ("plate-like organ") lying dorsally against body (Fig. 5f, g). Proximal half of limb unsegmented, distal half divided into 1 long and 5 short "articles," each with distal spinules; 2 small, complex spines at tip. Limbs 2–4 alike, progressively shorter (Fig. 5h–l). Long, fairly broad proximal article almost filled with long, flask-like seminal receptacles leading via narrow ducts to openings on proximal, nipple-like protrusion. Short, curved and tapered distal article lined with fine hairs; concave lateral edge with 5–6 short setae, tip with 5–7 setae, setulate ones slightly longer than others. Fifth pair very short, lobular, naked (Fig. 5m).

Furcal rami 3.5 times longer than high (Fig. 5n). No distal armament; 3 minute medial spines at regular intervals, distal 2 hirsute. Cuticle covered with short ctenae, longer near proximodorsal corner.

Remarks.—This specimen cannot be assigned to *B. hexapus* Pyefinch, *B. torrensis* Pyefinch, or *B. durbanensis* Brattström since it has a different number of thoracic limbs than they. The remaining species all have 5 pairs, counting the structure associated with the "plate-like organ" (Brattström, 1956), except for *B. digitatus,* which is transferred to a new genus below. Of the pertinent species, *B. japonicus* does not have coiled lateral mantle lobes, just a pair of simple sacs, and *B. verrucosus* Pyefinch has short, broad frontal horns, unlike the long, coiled ones at hand, and its plate-like organs are small (Grygier, pers. obs.). *Baccalaureus maldivensis* Pyefinch supposedly lacks the first limbs, but not the plate-like organs, and in *B. disparcaudatus* Pyefinch both structures are said to be absent (to judge from the holotype, which I examined, the first limbs and plate-like organs could have been lost in dissection). Both of these species also have terminal furcal setae, and the lateral carapace lobes coil less than the present specimen. *Baccalaureus pyefinchi* likewise has shorter lateral coils than this specimen and has terminal furcal setae. It supposedly has the last 2 pairs of limbs on the same segment, but this may be mistaken (see below). *Baccalaureus argalicornis* Brattström from Madagascar is only 50–70% as large as the present animal, and has furcal setae and 4 setae at the tip of the first limb, but otherwise is almost indistinguishable from the new specimen at the level of detail Brattström (1936; 1956) supplies. Personal examination shows that this species has darkly pigmented stippling and reticulations on the carapace which are lacking in the present specimen.

The new Polynesian *Baccalaureus* specimen differs from all described species in lacking terminal furcal setae and in having medial furcal spinules, although the latter are so small that they may have been missed in earlier studies. There may also be more setae on the thoracopods (details not reported for all species), and it is the first reported occurrence of biarticulate thoracopods in the genus (otherwise said to be unsegmented). Because of problems with the descriptions of those species most similar to the present specimen, it is not possible to decide whether or not this represents a new species.

I have adopted part of Brattström's (1956) model of the organization of the thorax in *Baccalaureus*: fundamentally 6-segmented; anterior horns arising from the first thoracomere, which is fused with the head; the plate-like organs regarded as excrescences at the bases of the first limbs; 3–5 additional limb pairs. However, I disagree with the necessity to invoke fusion of 2–3 posterior thoracomeres out of the original 6 in those species where Pyefinch (1934; 1936; 1937; 1939) counted only 4 or 5 thoracomeres. A critical examination of some of Pyefinch's descriptions and specimens shows that such a fusion has not occurred, even though the posterior limbs have been lost in most species.

For example, Pyefinch's (1939) drawing of *B. pyefinchi* (as *B. japonicus*) shows 4 thoracomeres, the first fused with the head; the anterior horns were supposed to be the antennules, and thus cephalic. With a recognition of their thoracic nature, and realization that the boundary of the first and second thoracomeres is often not well expressed (e.g., the present case), an additional anterior thoracomere is accounted for. To account for the sixth segment, it is only necessary to compare Pyefinch's drawing with Figure 5c. The so-called first abdominal segment in *B. pyefinchi* seems actually to be the last thoracic, and the so-called second abdominal segment is the first and second together, their articulation not drawn in and the penis misplaced anteriorly. The illustrations of *B. disparcaudatus* and *B. verrucosus* in the same paper show signs of the same misinterpretation. In the last case, the thoraco-abdominal boundary is drawn to make it appear that the penis arises from the second abdominal segment, an anomaly already commented on by Brattström (1956) and Wagin (1976). The suggested reinterpretation would add a limbless posterior thoracomere in these 3 species, thereby bringing them into conformance with *B. argalicornis* and the specimen from Raroia Atoll. Examination of type material confirms these suggestions. All 3 of Pyefinch's species actually have a 6-segmented thorax and 4-segmented abdomen with a penis on the first segment. Additionally, Brattström (1956) described how the limbs appear to be articulated to the segment behind their true position; it is likely that reports of 2 limb pairs on the same thoracomere (*B. torrensis, B. verrucosus*) are due to a similar illusion, and there is really no more than one pair of limbs per segment.

Tagmosis and limb arrangement no longer distinguish *Baccalaureus* species with 5 pairs of limbs. Size and mantle coiling likely vary with age, and the appendages are often inadequately described or based on too few specimens to be sure of their constancy. Redescriptions of several species of *Baccalaureus,* at least one based on a large number of individuals, are necessary to expose synonymies and to determine whether the French Polynesian specimen described here belongs to an established species, like *B. argalicornis,* or not.

Zoanthoecus new genus

Diagnosis (♀).—Carapace a rigid, oval sac higher than long or wide, with aperture on rounded, posterior protrusion at about midheight. Lateral, branching channels radiating from below posterior protrusion, leaving marginal pouches on each side. External cuticle papillose. Main body attached just below aperture, tagmosis 5-6-4. First thoracic tergite bounded front and back by transverse frill, expansion of arthrodial membrane; other tergites short with much arthrodial membrane between. Five pairs of uniramous thoracopods, first limb with plate-like organ at base. Posteroventral spines on last abdominal segment. Furcal rami several times longer than high with few terminal setae. Parasites of zoanthids.

(♂).—Large, anteroventral carapace pores. Thoracomeres 5 and 6 without dorsal setae. Thoracopods 1–5 with 1–3 exopod setae. Pair of posteroventral spines on fourth abdominal segment.

Etymology.—From the host taxon, Zoanthidea, and Greek *oikos* (house), referring to encapsulation by the host. Gender masculine.

Type Species.—*Zoanthoecus cerebroides* new species.

Zoanthoecus cerebroides new species
Figures 6, 7, 8a, b

Material.—Holotype ♀ (USNM 204745), allotype ♂ (USNM 204746), about 65 paratype ♀♀, 4 paratype ♂♂ (USNM 204747; Bernice P. Bishop Museum Cat. No. B508; authors collection), about 20 nontype ♀♀, long dead before collection: coll. M. Palmgren in 3 hauls 21–22-I-1978, Nihoa Bank, Hawaiian Islands (23°16–17′N, 162°37–38′W, 204–260 m). Host zoanthid *Gerardia* sp. (ident. R. Grigg) overgrowing unidentified gorgonian. All specimens except a few females had been dried (not holotype).

Diagnosis.—As for genus.

Etymology.—From Latin *cerebrum,* referring to the convoluted appearance of the carapace in the female.

Host–Parasite Interaction.—A female *Z. cerebroides* lives either within 1 *Gerardia* polyp or is enclosed within a cluster of them. It is difficult to remove the zoanthids in undried material without ripping the carapace of the parasite. Adhesion is effected by a clear, brittle, amber to dark brown skeletal secretion of the polyps which surrounds the old gorgonian axis and continues as thin extensions beyond the ends of the gorgonian branches, just as in *G. savaglia* in the Mediterranean (Roche and Tixier-Durivault, 1951). This secretion encapsulates the parasitizing ascothoracids as well, and remains as an empty cyst after the parasite dies. The carapace is not attached directly to the gorgonian axis by its anterior side, as in *Laura.* Rather the lateral side is usually stuck to the axis more or less strongly depending on the amount of skeletal secretion laid down around it by the *Gerardia.*

Most males were found in debris at the bottom of jars, so their relationships to the zoanthids and the females are unknown. I found 1 male within an old, broken cyst of a long-dead female; there is no way to tell if this is usual or accidental.

Females.—Carapace reniform, heavily wrinkled (Fig. 6a, b). Holotype 5.1 mm high (major axis), 4.0 mm long; dissected paratype 5.8 mm high, 3.8 mm long, 3.4 mm wide: dried specimens 2.1–5.4 mm high, length 0.65–0.85 times height (1.8–3.8 mm), width generally 0.45–0.65 times height. Mid-sagittal outline smooth with protrusion at midheight on posterior side, and deep, transverse groove below it. Channels fan out from this groove over both sides of carapace, pattern varying between individuals (and even sides of same animal), usually delimiting about 10 rounded pockets near periphery, fewer in smallest individuals. Branches of midgut diverticula, flanked by ovaries, run along bottoms of channels within carapace; peripheral pouches without such organs, serving as brood chambers for eggs and larvae (Fig. 6c). External surface with simple, round papillae. Vertical, slit-like aperture on posterior protrusion, pair of rounded projections flanking lower end.

Main body (Fig. 6d) fused broadly to carapace at inner end of transverse groove, where gut diverticula and ovaries come together and enter cephalon, and where carapace adductor muscle is found. Body 1 mm long in average specimen, higher than long because of dorsal frills. Head facing ventrally, bearing small antennules and oral cone, latter pointing toward anterior end of upper side of transverse groove. Thorax arched so posterior half and abdomen oriented toward aperture.

Antennules (Fig. 6e) nearly straight, about as long as oral cone, apparently 6-segmented, third and fourth articles small and obscurely demarcated. Tiny

Figure 6. *Zoanthoecus cerebroides* new genus and species; c, e–h, holotype ♀ (USNM 204745); a, b, d, i, paratype ♀ (USNM 204747); a, b, carapace, lateral and posterior views; c, cutaway view of carapace, showing organs and orientation of main body; d, main body, lateral view; e, antennule and frontal filament/second antenna; f, first limb (without plate-like organ) and detail of tip of another; g, third limb; h, fourth limb; i, abdomen with musculature. For explanation see Figure 1.

anterior seta on third (?) article and perhaps another near base of fifth. Sixth article with long, thick aesthetasc, reduced, sometimes spine-like claw guard, and narrow, uncurved distal claw (muscle attached posterior to it). Frontal filament or antenna at base of antennule seen only on one side of one dissected individual, probably

destroyed in other preparations; short stub with several digitiform processes (Fig. 6e).

Oral cone about equally long, deep, wide. Posterior edges of labrum meeting, but readily separable. Mouthparts as in *Laura.*

Thoracic tergites widely separated dorsally by arthrodial membranes. Membrane between first and second tergites produced dorsally and laterally into smooth, transverse frill. Smaller frill ahead of first tergite. Posterior edge of sixth tergite with band of setae.

Five pairs of thoracopods, apparently on thoracomeres 1–5, but close packing and lack of segmental boundaries in pleural region make this hard to ascertain. Limbs shorter posteriorly, fifth pair almost perpendicular to first because of thorax curvature. Aside from abundant fine hairs, setation limited to no more than 5 short, terminal setae. First limbs (Fig. 6f) narrow, cylindrical, not obviously segmented. Rounded lamellar protrusion of body wall (plate-like organ) at its base, folded posteriorly against body, genital papilla behind it. Limbs 2–4 relatively broader than first, not well segmented (Fig. 6g, h). Distal part probably exopod; vestigial endopod seen in one limb (Fig. 6h). Flask-shaped seminal receptacles in limbs 2–4, many in second limb, fewer in third, only 1 in fourth; other seminal receptacles in thorax above limb bases. Receptacle ducts open on low swellings at base of limbs. Fifth limb vestigial, without distal setae (Fig. 6d).

Sperm expressed from seminal receptacles as in *Laura dorsalis,* filiform, with apical acrosome, nucleus 18 μm long and about 0.75 μm wide, conical midpiece 3 μm long, and tail at least 30 μm long.

First abdominal segment the largest, dorsal side longer than ventral. Ventral sides of other 3 segments much longer than dorsal, causing posterior bend (Fig. 6i). First segment with band of fine, posterior setae, uniramous ventral penis arising from hirsute projection. Fourth segment with furcal rami and pair of small, complex, posteroventral spines. Furcal rami tapered, 2.5–3.5 times longer than basal height. Sparse ventral cuticular ctenae and 4 terminal setae; dorsalmost longest, over half as long as rami, ventralmost shortest, middle 2 intermediate and equal.

Males.—Carapace (Fig. 7a) bivalved, oval in side view, about 0.9 mm long, 0.55 mm high, 0.6 mm wide with valves closed, anteroventral parts of valves protruding with pore on nipple-like papilla. Most of outer cuticle with occasional setae and numerous spinules partly arranged in longitudinal rows (Fig. 7a); no spinules over adductor muscle insertion. Ventral edges of valves smoothly rounded with toothed ridges and sharper spinules than rest of carapace (Fig. 7b, c). Anteroventral pores 11 μm across, leading into pit 40 μm deep (Fig. 7d); inner end surrounded by halo of fine, radiating structures (canals in thick cuticular wall?).

Main body attached along anterior half of dorsal hinge (Fig. 7a, e). Head with large, prehensile antennules and oral cone. Six thoracic segments gradually longer and less high posteriorly, first one apparently fused to head, sixth beginning downturn of body; a pair of limbs per segment. Abdomen 4-segmented with much arthrodial membrane between segments, hanging vertically except for upturned fourth segment. First 3 segments about equally long, progressively narrower, first with very long penis; fourth longer with furcal rami.

Six-segmented antennules extremely large and powerful, extending at least twice as far as oral cone and longer and thicker than abdomen, folded at rest so second and sixth articles form top and bottom of Z. First article triangular, second parallelogram-shaped, third triangular. Fourth article short rectangle with 2 unequal,

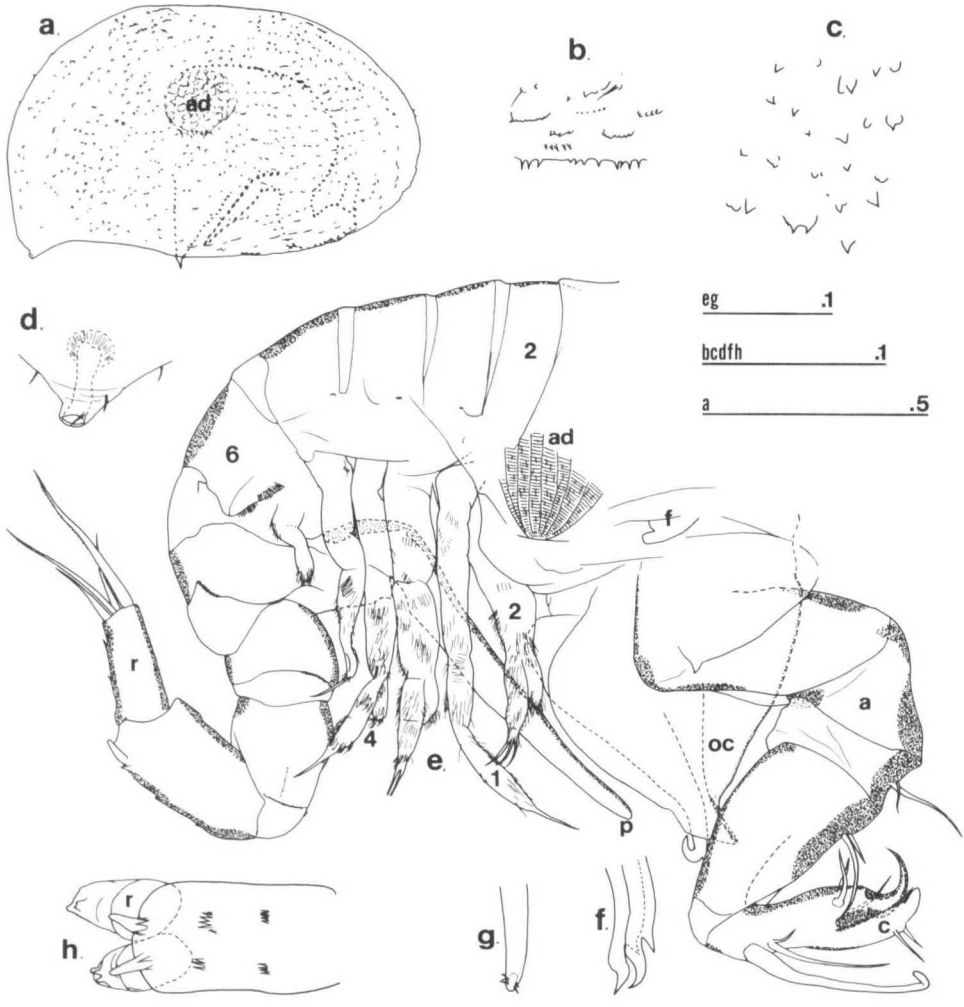

Figure 7. *Zoanthoecus cerebroides* new genus and species, paratype (USNM 204747); a, carapace, lateral view, body outline dotted; b, c, carapace spinules from near ventral edge and middle of side, respectively; d, anteroventral pore; e, main body, lateral view; f, tips of maxillae; g, tip of penis, ventral view; h, fourth abdominal segment and furcal rami, ventral view, setae omitted. For explanation see Figure 1.

anterior setae. Fifth article oblong, tapered, with 2 unequal, anterobasal setae. Sixth article ends in sharp claw with 3 setae at base; ventral side with, progressively closer to claw: aesthetasc as long as article; 1 long and 1 short seta arising together; long, laterally flanged claw guard with 2 short, ventrodistal setae, and diaphanous distal lobe accompanied by third short seta.

Small mound with distal lobe projects from inner carapace lining lateral to posterior end of antennular basal segment; this either a vestigial antenna or, probably, vestigial eyestalk (Grygier, 1983a), homologous to base of frontal filament in female.

Oral cone equilaterally triangular in side view with sharp, protruding tip. Uncertain whether posterior edges of labrum meet. Only obvious mouthparts in

undissected oral cones are maxillae, their bifid tips with movable posterior hook much larger than anterior prong (Fig. 7e, f). Maxillary gland ducts at bases of maxillae; paired ventral swellings between oral cone and first thoracopods contain the glands themselves.

First thoracopod uniramous, longer than other limbs, arising lateral to second thoracopod; segmentation indistinct, 3–4 articles; 1 short, distal seta; like all limbs, irregularly covered with short, fine hairs. Limbs 2–4 about equal, biramous, basis little shorter than coxa; exopod twice as long as endopod, with traces of 2 articles and 1–3 short, distal setae. Fifth limb as long as protopod of preceding limb, uniramous, with short, distal seta. Sixth limb uniramous, without setae, only as long as exopods of limbs 2–4. Lateral fringe of fine hairs on sixth thoracomere above base of limb.

Penis 2-segmented, uniramous. First article protrudes forward from ventral side of first abdominal segment to about level of third thoracopods. Distal article long, straight, tapered rod with thickened anterior side and several tiny hairs at tip (Fig. 7g).

Fourth abdominal segment with 3 paired sets of ventral spinules and pair of larger, blunt, posteroventral spines (Fig. 7h). Furcal rami half as high as last abdominal segment, twice as long as high, with 4 distal setae, 2 longer than others.

Developmental Stages.—Very few females were brooding. One specimen was full of eggs, and another had a few nauplii. Eggs subspherical, 0.22 × 0.19 mm (mean of 25).

Nauplii similar to *Laura* spp. in body form, frontal filaments, labrum, and armament of posterior end of body (and of next instar). Equatorial pores in single row. Antennules unsegmented, but setation as in *Laura.* Antennae and mandibles with protopods like *Laura,* exopod of former with about 9 articles and 5 setae, exopod of latter 6-segmented with 4 setae. Endopods of both vaguely 4-segmented with setae placed 2-0-2-3.

Isolated valve of bivalved crustacean which may be ascothoracid larva ("cyprid") of *Z. cerebroides* found in debris at bottom of one jar (Fig. 8a, b), nearly identical to carapace of ascothoracid larva described by Tessmann (1904) from Indian Ocean North Equatorial Current, and also to a single valve from the Red Sea illustrated by Bonaduce et al. (1983) and identified by them as an ostracod, *Rutiderma* (?) sp., probably mistakenly (Kornicker, pers. comm.). The present valve is 0.71 mm long, 0.41 mm high, oval except for large, posterodorsal concavity (Fig. 8a). Pronounced dorsolateral swelling. Round, yellow area above midheight at midlength of dorsal hinge line apparently corresponding to insertion of adductor muscle. Very pronounced hexagonal pattern to cuticle, individual cells about 12 μm across, with pores in small, circular cells at certain vertices (Fig. 8b).

Associated Fauna.—One of the 30 inspected females contained a damaged cryptoniscid isopod, apparently of the same undescribed genus, but a different species, than the hyperparasite of *Laura bicornuta.*

Two of the samples contained a few specimens of *L. bicornuta* itself, parasitizing *Gerardia.* Since some of the males and the ascothoracid larval valve described above came from the third sample, with no adult *Laura,* I do not think it likely that the males and larva really belong to *L. bicornuta.* This is the second record of 2 ascothoracid genera sharing a single host: a specimen of *Isidascus longispinatus* Grygier and *Thalassomembracis acanthosphaericus* Grygier were found on the same chrysogorgiid gorgonian north of the Bahamas (Grygier, 1984).

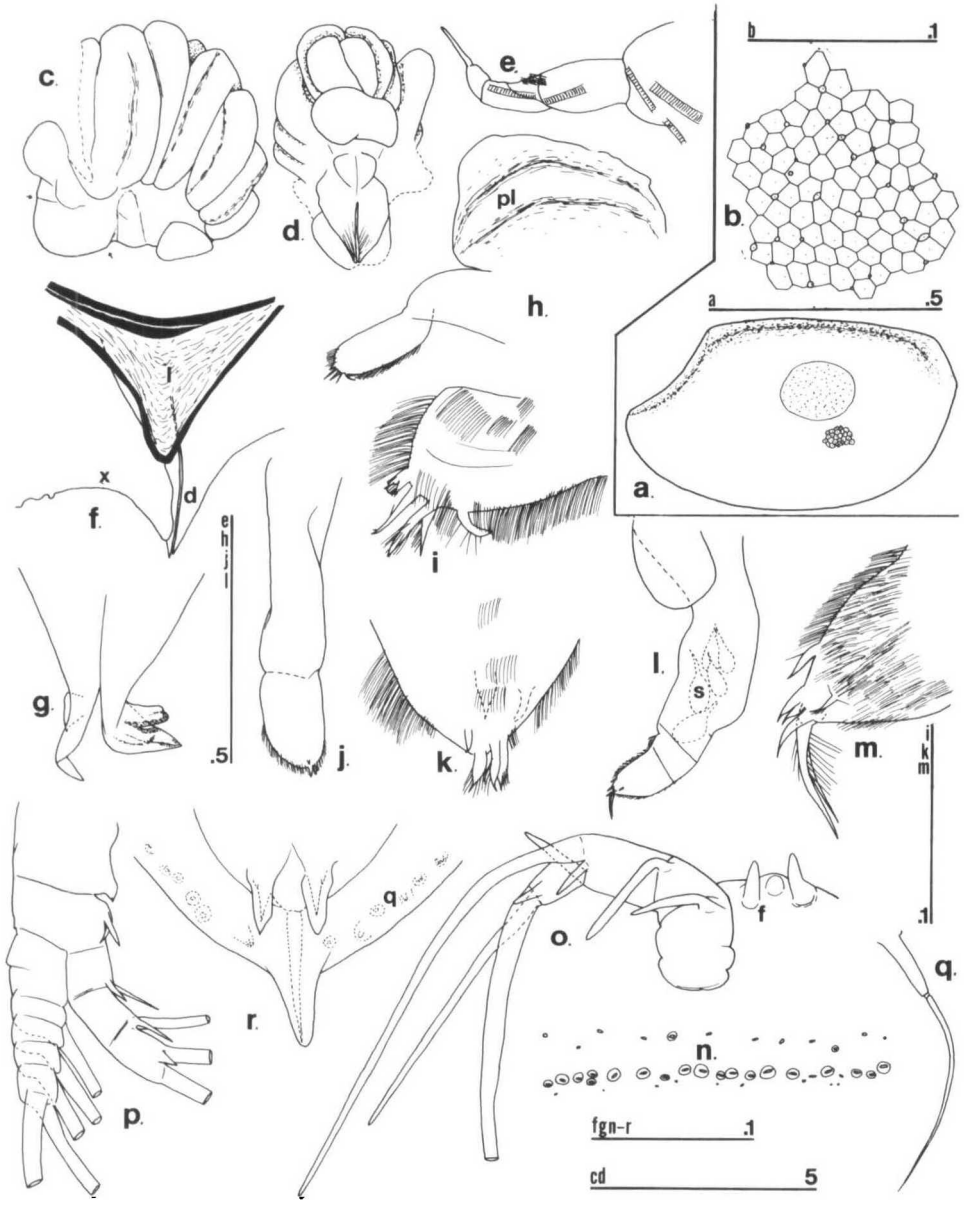

Figure 8. a, b, Carapace valve attributable to ascothoracid larva of *Zoanthoecus cerebroides* new genus and species; a, lateral view, adductor muscle attachment dotted, small area of cuticular sculpturing shown; b, enlargement of cuticular sculpturing at approximately center of valve. c–r, *Polymarsypus digitatus* (Pyefinch), new combination; c–m, holotype (BMNH 1940.85–87); c, carapace, lateral view, one pocket ripped away, aperture indicated by arrows; d, carapace, ventral view, ripped areas dashed; e, antennule; f, mouthparts except maxillae, ventral view, one maxillule missing; g, tips of maxillae; h, i, first limb and detail of its tip; j, k, second limb and detail of its tip; l, m, third limb and detail of its tip; n–r, nauplius; n, equatorial pores along part of lateral side; o, frontal filaments and antennule; p, antenna; q, post-mandibular appendage of next instar; r, posterior end of body. For explanation see Figure 1.

Remarks.—The carapace of *Z. cerebroides* is similar to that of *Laura* in its stiffness, overall form (ignoring the surface convolutions), and mode of attachment of the main body to the posterior side. Unlike *Baccalaureus,* which often lacks or has very small mandibles and maxillules (Pyefinch, 1936), these 2 genera have 3 well developed pairs of mouthparts of common construction. However, *Laura* and *Zoanthoecus* are certainly distinct.

Zoanthoecus lacks the rosette papillae that characterize the carapace of *Laura,* and the female does not have *Laura*'s full complement of 6 pairs of thoracopods. The distal antennular article is distinctive, *Zoanthoecus* retaining the claw and a small claw guard, while at least 2 species of *Laura* have suppressed the claw and have a larger claw guard. *Laura* never has a plate-like organ at the base of the first limb. The furcal rami are much longer relative to the height in *Zoanthoecus,* and in *Laura* the thoracic tergites are not widely separated by arthrodial membrane. Finally, the complicated contours of the carapace can be considered diagnostic of *Zoanthoecus.*

Except for the lack of frontal horns on the first thoracomere, and the spaces between the tergites, the main body of *Z. cerebroides* could be mistaken for a species of *Baccalaureus.* However, in that genus the body is attached anteriorly within the medial carapace lobe, and the carapace itself is divided into a pair of lateral sacs. This is a fundamentally different modification than seen in *Zoanthoecus* and *Laura.* Although the pouched carapace of *B. digitatus* is superficially similar to *Z. cerebroides,* and both species lack frontal horns, *B. digitatus* deserves a genus of its own (see below).

Lacaze-Duthiers (1883) described a bivalved larva or male of *Laura gerardiae* in insufficient detail for comparison with the present males. However, the male of *Z. cerebroides* is similar in most respects to that of *Baccalaureus japonicus* (Yosii, 1931; Okada, 1938).

In the latter, the carapace is smaller (0.6 × 0.4 mm), the smoothly rounded anteroventral part lacking papillae or pores. The antennules are like *Z. cerebroides* except for lacking 3 small setae that may have been missed. Yosii (1931) considered only the hooks projecting from the oral cone as the maxillae, and the straight points as the maxillules; this is in error since both are parts of the maxillae. Wagin (1976) cited Okada's (1938) drawing in an argument that the antennular claw in ascothoracids originated as a seventh article; in fact, he seems to have mistaken a seta at the base of the claw for the edge of a peduncle bearing the claw. The tagmosis and limbs are basically alike in the 2 genera, although Yosii (1931) saw 3-segmented protopods on the first 4 limbs and biarticulate endopods on limbs 2–4, unlike *Z. cerebroides.* Yosii (1931) said that the exopodites of limbs 2–4 each end in a short spine, but Okada (1938) does not so illustrate them. The presence of 1–3 setae distinguishes the present males. Yosii (1931) mentions 3 furcal setae in *B. japonicus,* but Okada (1938) illustrates 4. Neither author shows distinct posteroventral spines on the last abdominal segment. The last 2 thoracomeres have dorsal hairs in *B. japonicus,* but not *Z. cerebroides.* The penis is the same in both, but the easily missed distal hairs were not seen in *B. japonicus.* The Japanese authors described no eyestalk or antenna, not surprising since this structure is only visible if the carapace valve is folded back without much ripping.

The males of *Z. cerebroides* had been dried, so their internal structure could not be examined. Yosii (1931) saw possible oocytes ventrally in the valves of the *B. japonicus* males, and testes dorsally. Pyefinch (1936) considered this an aberration, because he mistakenly thought that adult *Baccalaureus* were simultaneous hermaphrodites (mistaking seminal receptacles for testes). Another interpretation is that Yosii's males, and the present ones, are the protandric stages of

sequential hermaphrodites. Such protandric hermaphroditism has been inferred in other anthozoan-infesting ascothoracids (Grygier, 1981b; 1984; Moyse, 1983). However, the strongest evidence for protandry has recently been refuted (Grygier, in press).

The similarity of the males of *Baccalaureus* and *Zoanthoecus* is an argument for the monophyly of the Lauridae as presently constituted. The long, biarticulate, uniramous penis and the 4-segmented abdomen are unique to males of this family. Protanders or males of such gorgonian-inhabiting genera as *Gorgonolaureus, Isidascus* Moyse, and *Thalassomembracis* Grygier, which seem to have some relation to the laurids, are more generalized, with a different, more setose antennular armament, paddle-like, heavily setose, biramous thoracopods, and a 5-segmented abdomen with a heavily setose furca (Grygier, 1981b; 1984; Moyse, 1983).

The anteroventral pores are one of the most interesting features of male *Z. cerebroides,* because till now such pores were known only in males and females of the very generalized, ectoparasitic genus *Waginella* Grygier (1983b). Cirriped cyprid larvae have similarly positioned pores, the exits of the "frontal horn glands" (Walker and Lee, 1976), but their homology with the present pores is not clear-cut (Grygier, 1983b). If anteroventral carapace pores are of independent origin in Cirripedia and Ascothoracida, then their peculiar distribution within the latter subclass might force a reappraisal of phylogenetic relationships within the Ascothoracida.

Polymarsypus new genus

Baccalaureus Broch, 1929, partim—Pyefinch, 1939: 247, Wagin, 1976: 112.

Diagnosis (♀).—Carapace thin-walled, sac-like, with series of dorsoventrally elongate, lateral lobes. Tagmosis 5-6-4. Dorsal setae on all 6 thoracomeres. Thoracopods uniramous, plate-like organs at base of first pair. Three other limb pairs, last 2 containing seminal receptacles and with large, flat lobes at base. Furcal rami elongate, tapered, with few distal setae. Parasites of zoanthids.

Etymology.—From Greek *poly* (many) and *marsypos* (pouch), for the series of lateral outgrowths of the brood chamber. Gender masculine.

Type-species.—*Baccalaureus digitatus* Pyefinch, 1939.

Polymarsypus digitatus (Pyefinch), 1939 new combination
Figure 8c–r

Baccalaureus digitatus—Pyefinch, 1939: 257, Wagin, 1976: 120.

Material.—Holotype ♀ with nauplii (BMNH Reg. No. 1940.85–87): *John Murray* Expedition Stat. 184, Gulf of Aden, 1,270 m, in unidentified zoanthid.

Diagnosis.—As for genus.

Redescription.—Carapace (Fig. 8c, d) thin-walled, soft, 5.3 mm long, 5.2 mm high, 3.3 mm wide. Aperture along midline of laterally compressed, posteroventral part, pair of low mounds anterior to it. Eight pairs of outpouchings (most anterior of which missed by Pyefinch, 1939), and transverse, anteroventral swelling. Pouches primarily anterolateral outgrowths of brood chamber (not dorsal, finger-like lobes), connected to main chamber by vertical slits. Nauplii found within pouches.

Main body (Pyefinch, 1939, text-fig. 18) 3.2 mm long, occupying ventral, unlobed part of carapace. Six thoracomeres dorsally hirsute (except anterior half of sixth), abdomen 4-segmented, first segment posteriorly hirsute. Four pairs of limbs

seen, apparently corresponding to thoracomeres 1–4; ventral part of posterior thorax damaged, but apparently no additional limbs.

Antennule (only 1 seen) 4-segmented, first article short and wide, second and third oblong with few cuticular ctenae, fourth short with seta (Fig. 8e).

Mouthparts as in *Laura dorsalis,* except medial, retrorse hairs of mandibles not visible in present preparation (Fig. 8f, g).

First thoracic limb short, directed posteriorly with fine distal hairs, few distal setae, and *Baccalaureus*-like plate-like organ at base (missed by Pyefinch, 1939, fig. 8h, i); latter about 0.42 mm long, 0.26 mm wide, running lengthwise below chitinous ridge and folded in two towards body. Second limb longest, 2-segmented, distal article with fine hairs and several setae (Fig. 8j, k). Third and fourth limbs alike, latter slightly shorter, 3(?)-segmented with several distal setae (Fig. 8l, m); 4–5 bottle-shaped seminal receptacles in protopod; large, flat, lateral lobe at limb base through which ducts of receptacles pass.

Penis on first abdominal segment thicker than Pyefinch (1939) drew it. Furcal rami elongate, tapered, with 3 distal setae on 1 ramus, perhaps none on the other.

Nauplii.—Shield-shaped in dorsal view, 0.62 mm long, 0.44 mm wide (mean of 5), dorsoventrally flattened, limbs short; condition immediately premolt, not within vitelline membrane as Pyefinch (1939) suggested. Equatorial pores in 3 rings, dorsal one widely separated from denser middle ring, with scattered smaller pores just below latter in ventral ring (Fig. 8n). Frontal filaments (Fig. 8o) short, conical, with bump between (vestige of nauplius eye?). Antennules as in *Laura* and *Zoanthoecus* in setal arrangement, at least 4-segmented (possibly also 2 short, basal articles), setae thick (Fig. 8o). Antennal coxa short with small enditic spine; basis short with 2 enditic spines; endopod 3-segmented, first 2 articles with 2 unequal medial setae, third with short spine and 2 long setae; exopod usually 7-segmented with 5 setae (Fig. 8p). Mandibles like antennae, except exopod generally with 1 less article and seta. Pair of long, setiform appendages of next instar (homologous with pair of setae in *Laura*) beneath cuticle behind mandibles (Fig. 8q). Rear end of body (Fig. 8r) with 2 ventral spines (similar spines of next instar within), and terminal spine (long seta of next instar within).

Remarks.—Although the lateral carapace pouches are reminiscent of *Zoanthoecus cerebroides,* the carapace is soft and pliable, the body attached anteroventrally within the carapace, and the posterior sector with the aperture compressed, in each case like *Baccalaureus. Zoanthoecus* and *Laura,* on the other hand, have a stiff carapace, the body attached mid-posteriorly due to a peculiar anteroventral development of the dorsal blood chamber, and a broad posterior projection bearing the aperture (Table 1). Wagin (1976) thought that *P. digitatus* was intermediate between *Laura* and *Baccalaureus* per se. This is not the case; it shows every sign of a close affiliation with *Baccalaureus.* However, *P. digitatus* should not be retained in that genus. It has neither of the derived characters that unite *Baccalaureus*: the anterior thoracic horns and a carapace divided into lateral lobes by a medial constriction. Possession of seminal receptacles only in thoracopods 3 and 4, and the large plates at the bases of those limbs, are unique to *Polymarsypus.* Every other laurid, and most other ascothoracids, have receptacles in the second pair of limbs as well.

The nauplius is a little different from the others described in this work (*Laura, Zoanthoecus*), and from *Baccalaureus japonicus* (Yosii, 1931), which are almost identical among themselves. The dorsal shield is flatter and larger, the limbs are shorter, and the endites are much feebler. *Baccalaureus maldivensis* and *B. hexapus* nauplii have fewer exopod setae than *P. digitatus,* but their limbs are quite long relative to the body, like the other laurids (Pyefinch, 1934; 1936).

Discussion

Morphology.—Table 1 lists a number of morphological features that distinguish the 4 laurid genera, according to current knowledge. The following is a list of apparent diagnostic features (synapomorphies) of the family Lauridae possessed by all genera: female carapace valves fused except for small aperture posteroventral to body; vestigial antennules in females, segmentation partly obliterated; more or less bulbous oral cone, labrum closed behind with spout-like tip; thoracopods uniramous (vestiges of endopods rarely present); abdomen 4-segmented in both sexes; penis uniramous; furcal rami tapered with few (rarely none) short, terminal setae. The medially hirsute, pointed mandibles and blunt, triangular maxillules might also be diagnostic if they can be shown to exist in *Baccalaureus.*

Although it is clear that the anterior horns of *Baccalaureus* are part of the first thoracomere and are not cephalic appendages, their nature is still controversial. Moyse (1983) supposed that they are homologous with the "filamentary appendages" at the bases of the first limbs in *Isidascus bassindalei* Moyse (Grygier, 1983d; 1984). These unarmed, elongate, anteriorly directed protrusions lie dorsal to the adductor muscle like the horns of *Baccalaureus.* I believe them to be homologous with the plate-like organs, however, since these protrusions are more closely associated with the first limbs than the horns are (Brattström, 1956). The horns are more likely another set of outgrowths of the first thoracomere, as illustrated by analogy with the two new species of *Laura. Laura gerardiae* has no trace of horns. In *L. dorsalis* the anteriorly bent, dorsolateral projections of the first thoracomere are clearly serially homologous with the smaller protrusions of the second segment. Simply by elongation, such protrusions could have come to resemble the anterior horns of *L. bicornuta* and, a step beyond, *B. verrucosus.* Coiling of these longer horns leads to the situation in other species of *Baccalaureus.* This is not to say that *Laura* gave rise directly to *Baccalaureus,* but the unbroken series of intermediate conditions leading to long, coiled, anterior horns is evidence of an origin apart from "filamentary appendages."

Biogeogaphy.—Till now *Laura* has only been known from the Mediterranean. The two new species described here, from Hawaii and Florida, indicate that the genus may have a Tethyan distribution. The other three laurid genera belong to the Indo-west Pacific faunal province, although the monotypic genera *Zoanthoecus* and *Polymarsypus* are so far found only at the geographical extremes (Hawaii and the Gulf of Aden, respectively). The previously recognized eastern boundary of the range of *Baccalaureus* ran from Japan to Vietnam to the Torres Straits. The present record from French Polynesia extends the genus much of the way across the Pacific, and it no doubt occurs in reef zoanthids throughout the tropical western Pacific. It is still unknown in the eastern Pacific or Caribbean where apparently suitable zoanthids are also abundant.

Wagin (1970; 1976) proposed a historical biogeographical scenario for the Ascothoracida. According to his history of the Lauridae, in the Paleozoic the western Tethys (Mediterranean) was inhabited by *Laura,* judged to be primitive. This had spread into the Eastern Tethys by the Middle Mesozoic and evolved into *Baccalaureus, B. digitatus* representing an intermediate state. *Baccalaureus* spread eastward through Tethys to Japan and southward between Africa and Lemuria (continent south of Tethys connecting India and Madagascar), and the latter representatives formed a center of speciation off southeastern Africa.

This model has obvious geophysical flaws, and the proposed sequence of evolution from *Laura* through *Polymarsypus* to *Baccalaureus* is not entirely plausible. More importantly, Wagin has an implicit assumption that is inadvisable for poorly sampled groups like the Ascothoracida. He takes the known distribution as the

actual distribution in his analysis. Now that *Laura* is found circumglobally and *Baccalaureus* is not limited primarily to the rim of the Indian Ocean, Wagin's entire scenario is insupportable (additional comments in Grygier, 1981c; 1983d).

Acknowledgments

I thank the following for loaning me specimens for examination: Drs. F. M. Bayer and S. D. Cairns (USNM), R. W. Grigg (Hawaii Institute of Marine Biology), G. A. Boxshall (BMNH), and M. J. d'Hondt (NMHNP). Dr. W. A. Newman (SIO) provided laboratory facilities, critical reviews of earlier drafts of the manuscript, and financial assistance for illustrations. An anonymous reviewer corrected my classical grammar. I gratefully acknowledge the assistance of Dr. H. Zibrowius (Station Marine d'Endoume), Dr. P. F. S. Cornelius (BMNH), Dr. L. S. Kornicker (USNM) Mr. C. Arneson (SIO) in various facets of this study, which was partly supported by NSF Grant DEB78-15052 and an SIO travel grant. This is a Contribution of Scripps Institution of Oceanography, new series.

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DATE ACCEPTED: January 5, 1984.

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